

6.—Plant Ecology of the Coastal Islands near Fremantle, W.A.

By W. M. McArthur*

Manuscript accepted—17th March, 1956

The plant communities of the major coastal islands near Fremantle, W.A., have been described in relation to the soils, climate and geomorphology and a comparison drawn between the island vegetation and that of the adjacent mainland.

The vegetation, which is structurally a *Scrub Formation*, is composed of three well defined sub-formations, viz., tall scrub, scrub and low scrub and several other sub-climax communities of doubtful status.

The island vegetation is of special interest, not only for its density of cover and high frequency of dominants, but also for the paucity of plants of the Myrtaceae, Papilionaceae and Epacridaceae and the complete absence of members of the family Proteaceae.

It has been shown that within one locality the distribution of species is dependent on habitat and for comparable habitats on the islands and the mainland the composition of vegetation is substantially the same. The overall distribution of species is explained by a late Pleistocene land bridge between the islands and the mainland.

Introduction

The vegetation of the coastal islands—Garden, Rottnest and Carnac—is very unusual when compared with that of the adjacent mainland. This fact has long been recognized and commented on both by local and visiting botanists, but apart from notes on brief excursions no account has been written. The object of this paper is to give a description of the vegetation of the islands and to discuss briefly its relationship to the environmental factors. In addition, a comparison is made between the vegetation of the islands and that of the coastal areas on the mainland between Rockingham and Scarborough. This has led to a discussion of the present distribution of species in the area and an interpretation of the past history of the islands in the light of this distribution. The geographic relation of the islands to the mainland is shown in Fig. 1.

Garden Island has been chosen for a more detailed study than the other islands because it has remained almost unchanged by settlement. Rottnest Island has been inhabited from the early history of the State and so has suffered drastic changes in vegetation; and Carnac Island, though its vegetation is unchanged, is considered too small for any but shoreline conditions to prevail.

The historical records of these islands can be traced back to 1658 (Heeres 1899), when a Dutch vessel, the *Waekende Boeij*, while looking for survivors of a ship which was wrecked further to the north, anchored to the north of a small island in latitude 31°47' S. Samuel Volkersen, the captain of the vessel, writing to the Governor of the East India Company in 1659, wrote:—

In slightly under 32° south latitude there is a large island at about three miles from the mainland of the Southland. The island has high mountains with a good deal of brushwood and many thorn bushes so that it is hard to go over Slightly more to the southward is another small island.

There is no doubt that Volkersen referred to Rottnest and Carnac Islands, although they were not named until much later.

In 1696 three vessels under the command of William de Vlamingh, while searching for a lost vessel, arrived at Rottnest Island and Gerrit Col-laert, captain of one of the vessels, wrote:—

On 31st December (1696) I again put on shore with the skipper I found several sorts of shrubs the greater part of which were unknown to me There were also a variety of trees and among them one sort the wood of which had an aromatic odour

and a few days later de Vlamingh wrote of:—

a very agreeable belt of trees, very thick and about half a league in extent We perceived that a very grateful odour came from these trees.

This quotation suggests that the vegetation of Rottnest Island has changed considerably and in fact *Callitris robusta* thickets were probably originally widespread. Garden and Carnac Islands are apparently unchanged and although Garden Island was studied by a zoologist from the French ship *Naturaliste*, little useful information on the vegetation can be obtained from his journal.

* Botany Department, University of Western Australia; Present address: Division of Soils, C.S.I.R.O., University Grounds, Nedlands, W.A.

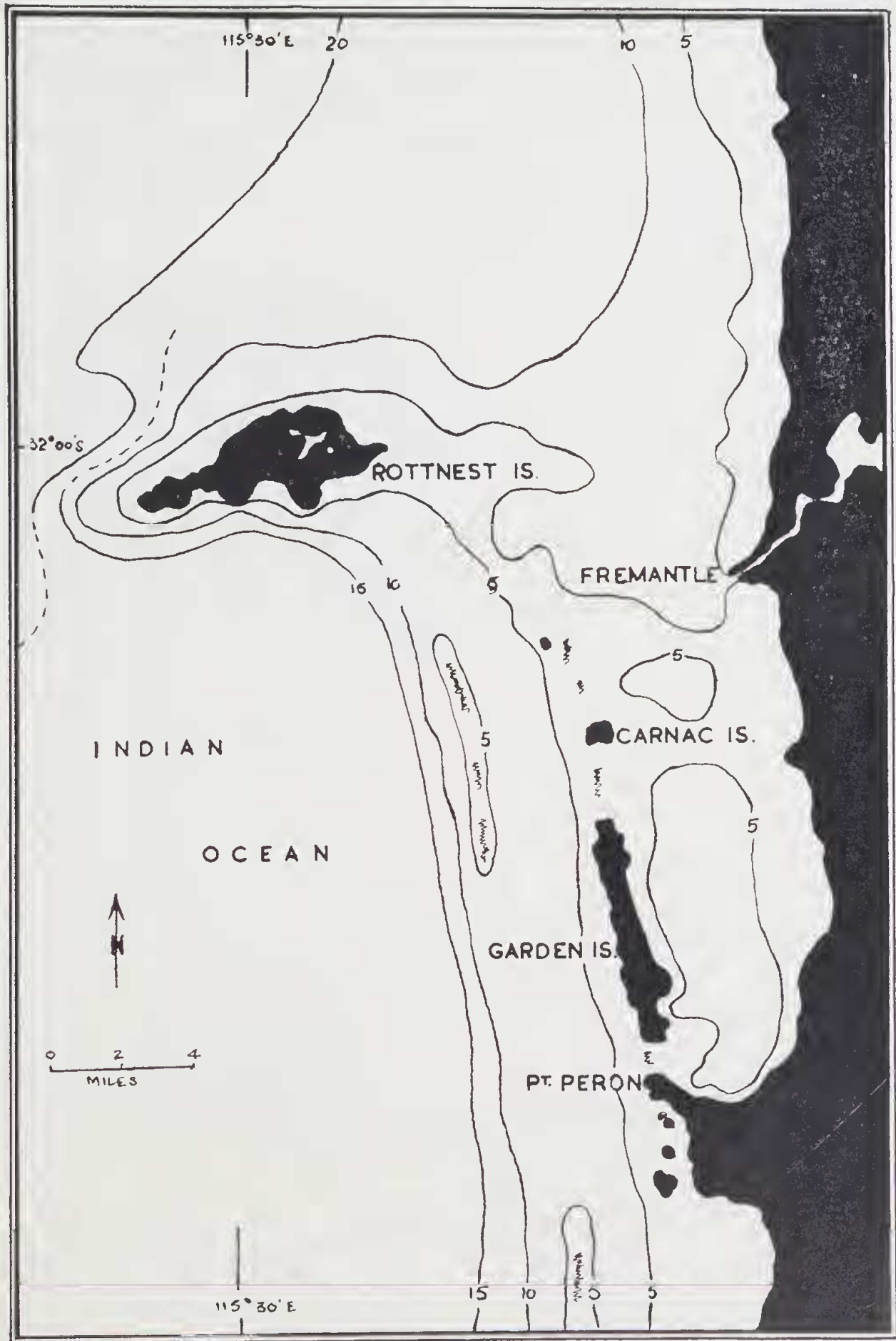


Fig. 1.—Plan showing location of islands and bathymetry of the surrounding ocean.

In 1854 William Harvey visited the area and writing of the vegetation of Rottnest Island said:—

... its land flora is remarkable for the total absence of Proteaceae and Grass trees and for the paucity of Myrtaceae, Epacridaceae and Leguminosae

Harvey's statement puts the problem in a nutshell, and it is the consideration of this problem, accompanied by a description of the environmental factors, which make up this paper.

A list of species and their distribution on the islands is given in Appendix I. The authorities for all species are also included in this list.

Geomorphology

The islands under discussion are parts of two physiographically distinct ridges which lie roughly parallel to the mainland coast between 32° and 32°30' south latitude. The easternmost ridge passes through Murray Reefs, Penguin and Seal Islands, Point Peron, Garden and Carnac Islands and the Stragglers. The other, about two miles further west, passes through Coventry Reef, Hawley and Casuarina Shoals and Rottnest Island. A study of the bathymetry of the region makes this feature even more marked (Fig. 1). These ridges are composed of Pleistocene to Recent aeolianite. They have been described (Teichert, 1947b; Fairbridge 1950) as being the remnants of a peninsula which extended about twenty miles from the present coastline when the level of the sea was considerably lower. With the rising of the sea the ridges have become more and more dissected until now there remain only four major land surfaces and several small rocky islands. Erosion is still going on, but only slowly. Point Peron has since been reunited to the mainland by blown sand (Fairbridge, 1948).

The islands have a hard core of travertinized calcareous dune rock which is generally taken to be late Pleistocene in age (Fairbridge, 1948). This rock is exposed extensively on Rottnest and Carnac Islands while on Garden Island it is largely blanketed by more recent sand dunes.

Exposures in the dunes on Garden Island show the typical cross-bedding of aeolianite. The upper 6-8 feet is still quite loose, but below this there is incipient cementation and a few travertinized root channels (Fig. 2). Analysis has shown that the lower levels are only slightly richer in calcium carbonate than the surface.

Garden Island can be divided into two physiographically distinct areas. The first is the main axis consisting of relatively high steep dunes underlain by limestone and the second is the low flat area making up Colpoys Point. It is suggested that the latter was formed comparatively recently by progressive additions of sand which washes through South Passage. This is indicated by the radial structure of Colpoys Point and the smooth even curve of Careening Bay.

A feature of the coastline, both on the islands and the mainland, is the presence of wave cut platforms at different levels above the existing sea level. Fairbridge (1948) has shown that

there is a fair degree of correlation between the raised platforms here and at Houtman's Abrolhos Islands 300 miles to the north. This suggests eustatic changes in sea level. The changes can be roughly referred to world-wide changes since the Pleistocene period (Zeuner, 1945, 1946). This allows of accurate dating of physiographic events in the area, the time of the 10 foot platform having been put at 2,000 B.C. The sea level apparently reached its maximum height at that time and has since dropped, with periods of stillstand at 5 feet and 2 feet. From this it can



Fig. 2.—Soil profile in a cutting through a dune. Solution channels are forming in the lower layers. Garden Island.

be assumed that individual islands and the mainland have not been linked by a direct land bridge for at least 4,000 years, and that probably the time when they were connected lies nearer 100,000 years ago. This would correspond with the Würm exposure of Europe.

There is no permanent fresh water on the islands and no evidence that there has been any in the past. However, the army authorities have put down two deep bores and several wells. The bores are artesian and there is a continuous flow of water to the sea.

Early visitors were unanimous in describing the islands as being mountainous, the steep and densely vegetated dunes giving an exaggerated impression of height when viewed from a distance. However, the highest point on Garden Island is slightly less than 200 feet, while Rottnest Island has a maximum elevation of 130 feet.

Climate

The area in the vicinity of Fremantle has a typically Mediterranean climate. In other words, there is a cool wet period and a warm dry period, with short periods of transition.

Most of the climatic data were obtained from the Rottnest Island weather station (see Appendix II) and it has been assumed that these records apply equally to conditions on Garden and Carnac Islands and Point Peron.

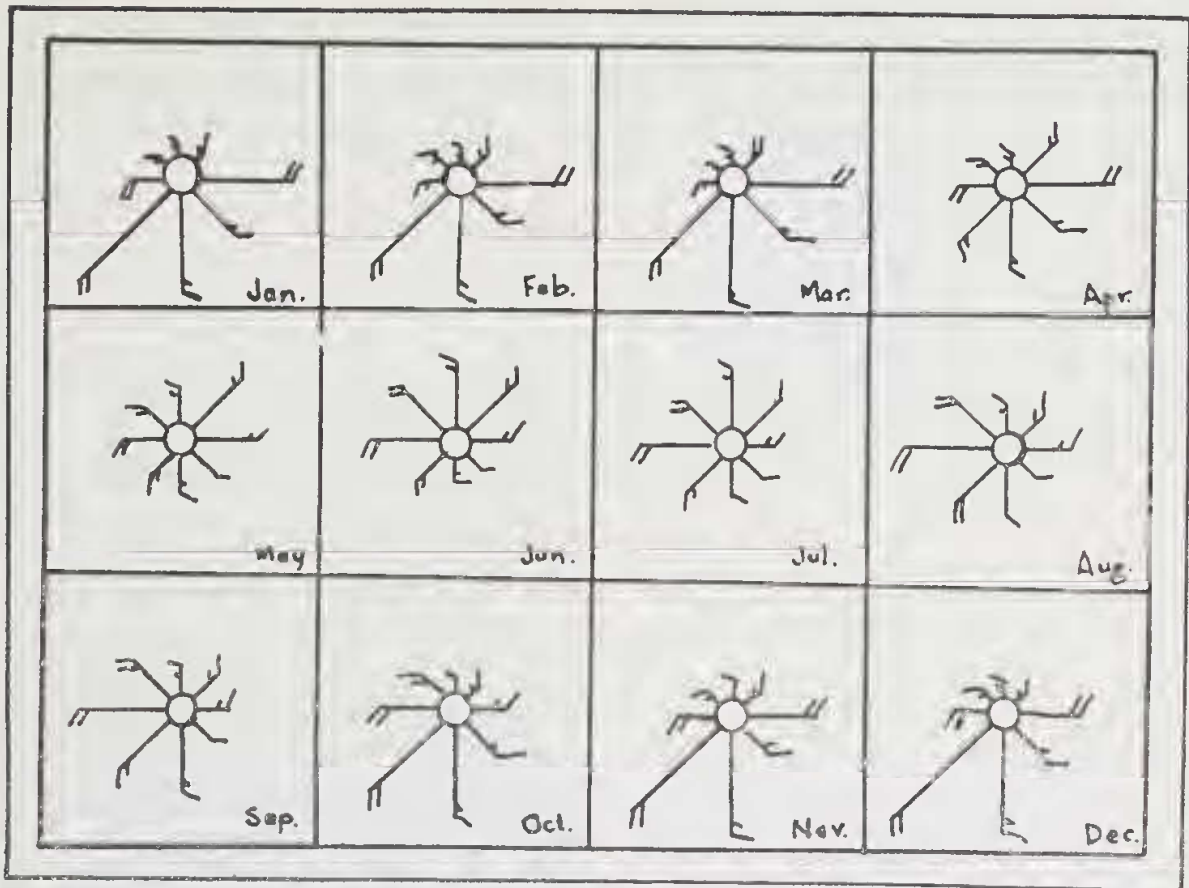


Fig. 3.—Mean monthly wind Roses at Perth Weather Bureau. The length of the arrows represents the mean total number of miles from each direction on a scale of 1in. to 5,000 miles. The feathers indicate the speed of the wind on the Beaufort Scale. North is towards the top of the page.

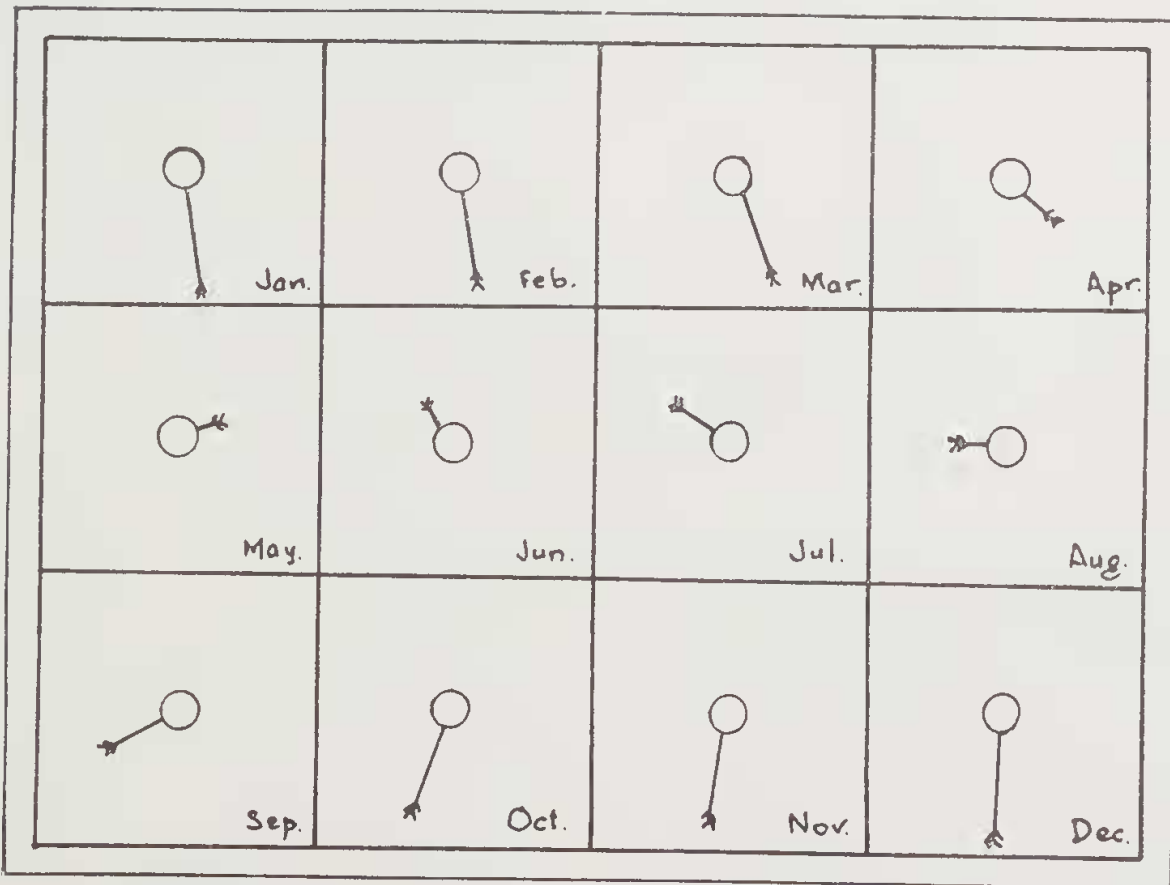


Fig. 4.—Resultant wind. Perth Weather Bureau. The length of the arrows represents the resultant wind on a scale of 1in. to 10,000 miles. North is towards the top of the page.

It is only during the period May-August that the west coast of Australia is subject to any constant rain-bearing wind. Rottnest Island receives 72% of its annual rainfall during these months and 93% during the months of April to October. Thus the distribution of rainfall is more important than the yearly total. During the winter there is a surplus while during the summer there is a marked deficiency. As the main rain comes when evaporation is at a minimum and run off is negligible in the loose sand most of it penetrates the soil. The figures quoted for potential evapo-transpiration (Appendix II) are calculated from a formula proposed by Thornwaite (1948). It is suggested that conditions in undisturbed scrub are such that the actual water loss would be less than the figure calculated.

The effectiveness of the rainfall was calculated using Thornwaite's (1931) formula, which is regarded by Gentilli (1948) as being the most suitable for Australian conditions. Rainfall effectiveness increases very rapidly during the latter part of April and decreases just as rapidly in August. This leaves about half the year when conditions become semi-arid or drier (less than 2.2). There is some lag, however, and it has been shown (Speck, unpublished data) that some soil water is still available until early December. On Garden Island the position of the ground water table varies from 4 feet below the surface in August to 14 feet in March.

It is suggested that plants obtain much of their moisture during the summer months from dew which forms every night, but which is never measurable. Wallabies (*Setonix brachyurus* and *Protemnodon eugenii*) have existed on the islands for centuries without any reliable fresh water supplies, suggesting that in summer the dew must be considerable. The greater part of Garden Island is covered with dense low scrub and this may have the effect of decreasing evaporation from the soil surface.

The lower mean monthly temperature limit for plant growth lies between 45° and 50°F. Since the lowest mean temperature on the coastal islands is 58°F. in July it may be concluded that temperature would, at the most, cause only a slight retardation of growth. It is also significant that the lowest recorded temperature is considerably above freezing point. A striking feature of the temperatures of the islands is the uniformity of the mean temperature. The daily range varies from 10° in July to 13° in February.

Wind data for Western Australia are limited, Perth Observatory being the only coastal station having a continuous record of wind speed and direction. However, it is considered that the wind at Perth would be substantially the same as on the coastal islands, except that sea breezes would begin to blow earlier each day and the velocity of the westerly and south-westerly winds would be greater than at Perth.

It will be seen from the monthly wind roses (Fig. 3) that for the nine months from July to March the greater part of the wind is from the south-western sector. This is due partly to the influence of the local winds, but also to the fact

that for some of this period the cyclonic winds coincide with the local winds. During April the predominant wind is from the east and May and June are almost equally windy from all directions. The diagram was constructed from records taken over ten years.

It is significant that the "resultant wind" (Fig. 4), which has been calculated for each month from the wind roses, reflects the control of the local winds for the greater part of the year. The cyclonic winds only become dominant during the winter months. Vegetation on the west coast of Garden Island is often aligned in a south-west north-west direction showing the predominating influence of the local winds (Fig. 5). The fact that the resultant wind makes a complete counter-clockwise rotation during the year is explained by the annual change in position of the belt of high pressure systems.



Fig. 5.—Cliff side vegetation, shaped and prostrated by wind action. Pt. Atwick. Garden Island.

The long axis of Garden Island is orientated about 15° west of north, while Rottnest has its greatest extent east-west. The importance of this becomes apparent when the prevailing winds are considered. It means that for Garden Island the maximum length of coastline is almost at right angles to the wind for the greater part of the year, while it is only the south-west portion of Rottnest which is affected.

The contrasting orientation of the islands may explain why Garden Island is largely covered by loose blown sand, while Rottnest has extensive rock outcrops.

On the west coast of Garden Island the effect of wind is very marked. Blow-outs and partial burying of the vegetation (Fig. 6) are common, and it is only those plants which can keep pace with the banking sand which survive. On exposed dunes and cliffs many shrubs have been reduced to a prostrate form by the action of the wind, each bush having a clipped appearance. The effects of salt spray on this vegetation must be considerable, especially where the waves break on rocks and the spray is carried over the land by wind.

Another wind effect may be seen in the orientation of *Callitris robusta* clumps on the north end of Garden Island (Fig. 7). From available evidence it is suggested that this clump has been spread through the seeds being blown by the wind. Ring counts of trees from different parts of the largest clump indicate that the

growth is at a minimum with the result that some plant groups are excluded or restricted. The family *Gramineae* for instance, which requires rainfall in the warm season, is represented by only one native species (*Stipa variabilis*).

Garden Island

The vegetation of this island is remarkable for three reasons. Firstly, certain important families of the mainland are either absent (*Proteaceae*) or present in restricted numbers (*Myrtaceae* and *Papilionaceae*). Secondly, the dominant species present show an unusually high frequency, five-sixths of the area available being covered by dense scrub formed by *Acacia rostelifera*, *Callitris robusta* and *Melaleuca hucgelii*. The third unusual feature of this vegetation is its structure which is probably unique in Western Australia. In many cases the scrub consists of a single storey of dominants in contrast to the three distinct stories found in the *Eucalyptus marginata* and *E. gomphocephala* communities of the mainland (Speck 1952). The closed canopy of the island vegetation serves further to distinguish it from any other community.



Fig. 6.—“Blowout” on the west coast of Garden Island. Sand is rapidly encroaching on to stable vegetation.

direction of the spread has been towards the north-east. During the summer months when the seeds are being shed the winds are from the south-west.

In this connection it is of interest to note that on the islands there are other species whose seeds are distributed by the wind. Some of these are *Senecio lautus*, *Arctotheca nivea*, *Clematis microphylla* and *Comesperma integerrimum*.

On the mainland the effect of wind has in certain areas been increased by the action of man. At Point Peron clearing of vegetation has led to mobile sand which is now fairly extensive. Attempts are being made to stabilise this sand by the introduction of Marram grass (*Ammophila arenaria*). Along the coast proper, especially on the wide, sandy beaches, the sand is constantly shifting and blow-outs are frequent.

It can be seen from the foregoing that the wind, although ordinarily not strong enough to uproot trees or break branches, has, by its very constancy, perhaps a greater influence than many of the other factors.

The effects of light, embracing intensity, length of day and duration of sunshine, form an important component of the environmental complex but without controlled conditions it is impossible to isolate its influence. It is reasonable to assume that it is the low light intensity which excludes most undergrowth from the dense *Acacia rostelifera* and *Callitris robusta* communities. On the other hand it is difficult to say whether it is the lack of competition or protection from the sun which allows the small annual *Didiscus* to flourish in the *Callitris robusta* thickets.

The salient point to be made in this very brief discussion of the climatic factor, is the seasonal aspect of the weather. The rain comes in the cooler part of the year when the rate of plant

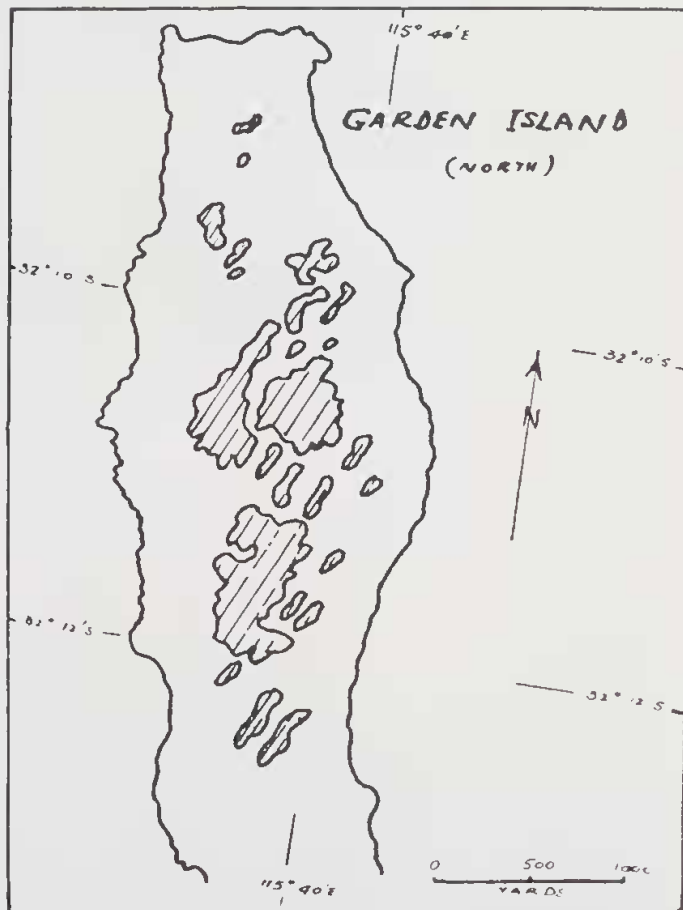


Fig. 7.— Lineation of *Callitris* clumps on North end of Garden Island. Traced from an aerial photograph.

The vegetation on the island consists of two ecologically and physiognomically distinct types: a stable central area of dense scrub and an unstable fringing zone. The fringing vegetation is subject to constantly changing conditions and this is reflected both in the structure and composition.

Using the system of classification of Beadle and Costin (1952) the following eight plant communities are recognised on Garden Island:—

- (i) *Callitris robusta* association (tall scrub)
- (ii) *Acacia rostellifera* association (scrub)
- (iii) *Melaleuca huegelii* association (scrub)
- (iv) *Myoporum insulare* association (low scrub)
- (v) *Acacia heteroclita* association (low scrub)
- (vi) *Pittosporum phillyraeoides* association (low scrub)
- (vii) Seasonal Communities
- (viii) Littoral Vegetation

The following discussions will apply to relatively pure communities although it must be stressed that in respect to the tall scrub and scrub communities there are all combinations from 100% of one to equal proportions of *Acacia rostellifera*, *Callitris robusta* and *Melaleuca huegelii* and often an admixture of *Melaleuca pubescens* and *Spyridium globulosum*.

Description of the Communities

Callitris robusta Association.—This community is restricted mainly to a large clump covering about a square mile in the northern part of the island. There are however small clumps in the *Acacia* scrub of the south end of the island and on the eastern extremity of Colpoys Point there is a mixed stand of *Callitris robusta* and *Melaleuca pubescens*. The average height of the trees in these clumps is 17-20 feet although many individual trees in the open grow to 35 feet. The average stem diameter is 2-3 inches and as most of the trees are 30-40 years old it is apparent that the annual increments are very small. In the clumps the trunks are straight and unbranched and the canopy completely closed giving the community the structural characteristics of a forest (Fig. 8). The undergrowth is very limited, *Phyllanthus calycinus* being the only common undershrub. In season, the tiny annual *Didiscus pilosus* flourishes in the *Callitris* community. The lack of light is possibly sufficient to restrict most other plants. There are isolated bushes of *Spyridium globulosum* and rarely *Eremophila brownii* and *Leucopogon richiei*. There are



Fig. 8.—*Callitris robusta* association, Garden Island. Note single storey structure.

occasional trees of *Melaleuca pubescens* and *Acacia rostellifera* and these have taken on the same form as the *Callitris* viz. tall and slender with only a tuft on top. The creepers *Cassytha glabella* and *Comesperma integerrimum* are present, but do not attain any large size. Within the community seedling regeneration of *Callitris* appears to be restricted, only a small percentage of those germinated surviving beyond December.

As far as can be seen there is no obvious factor limiting the distribution of *Callitris*. It grows as individual trees and small clumps throughout the *Acacia* scrub. It is scattered through the *Melaleuca huegelii* community and it competes on equal terms with *Melaleuca pubescens*. There is evidence that the *Callitris* is encroaching on the *Acacia* scrub. Ring counts of trees from different parts of a clump show that the age decreases from 40 years in the centre to 22 years at the periphery. This indicates that the spread of the clump has been a gradual process. It is significant that the boundary between these two communities is quite sharp. There is seldom any merging one into the other.



Fig. 9.—*Acacia rostellifera* association showing the dense, uniform canopy. *Stipa variabilis* and *Didiscus coeruleus* are shown at the side of the track. Garden Island.

A feature of the *Callitris* scrub is the thick layer of leaf litter. There is commonly 2-3 inches of undecomposed leaves on the surface below which is about 1-2 inches of decomposing leaves. The soil profile below this is as follows:—

- 0-1in. Dark grey calcareous sand rich in organic matter
- 1-6in. Grey-brown calcareous sand
- 6-45in. Light yellowish grey calcareous sand becoming very light grey with depth

Table I shows that the nutrient status of the soil is very high for natural conditions.

Acacia rostellifera Association.—This is the most widespread community on the island. Superficially the impression is given of a pure stand, but *Callitris* occurs throughout and *Melaleuca huegelii* forms an integral part. *Melaleuca pubescens* also appears sporadically, while *Spyridium globulosum*, which often attains a height of 8 feet, must be considered as a co-dominant.

The *Acacia rostellifera* scrub is very uniform in height (8-10 feet) and extremely dense and tangled (Fig. 9). Other species of *Acacia* are present, e.g., *Acacia cyanophylla* and *Acacia heteroclita*. The former, while of rare occurrence, is spread throughout the association, while the latter is mainly present in the vicinity of the mobile dunes.

Undergrowth is usually present even though restricted in many parts to *Stipa variabilis*. *Phyllanthus calycinus* and *Acanthocarpus preissii* occur in the more open areas. *Leucopogon* spp. and *Diplolaena dampieri* grow where the scrub thins out to separate bushes. *Guichenotia ledifolia* and *Lasiopetalum angustifolium* occur towards the northern end of the island in less dense areas, and *Didiscus coeruleus* (Rottneist Daisy) grows profusely where the scrub has been cleared.

Acacia rostellifera scrub shows a remarkable ability to regenerate vegetatively, exposed or damaged roots giving rise to new bushes. Many roads made by the Army during the period 1939-1945 are now completely over-grown and the scrub constantly encroaches on any cleared area. It appears to be a very vigorous community.

The soil is brown and powdery below the layer of decomposing leaves and at 2 feet is very light grey calcareous sand (Fig. 2). The important point about this soil is that it supports a very dense vigorous vegetation suggesting that the nutrient status is high. Chemical analyses (Table I) show a very high nitrogen level which may be due to symbiotic nitrogen fixation. No clear-cut evidence has been obtained to indicate nodulation here. It may, however, be noted that Wilson (1939) in U.S.A. has shown that some *Acacias* do possess *Rhizobia* as do also some species in Queensland (McKnight 1949). Root nodules have been noted on several species of *Acacia* found in the vicinity of Perth (Parker, personal communication).

Melaleuca huegelii Association.—This association is confined to several small areas to the north of Sulphur Jetty near the eastern coast of Garden Island where it is developed on low lying areas. The canopy is very uniform and its density is increased by the ereepers, *Cassytha glaberrima*, *Clematis microphylla*, *Comesperma integerrimum*, *Rhagodia baccata* and *Hardenbergia complanata*, which flourish here. There is a well defined under-storey of shrubs consisting of *Eremophila brownii*, *Phyllanthus calycinus*, *Acanthocarpus preissii* and *Leucopogon richiei*. Below this is a thick mat of moss and in spring the annuals *Didiscus pilosus* and *Pariclaria debilis*.

The soil has a fairly high concentration of organic matter below a thin layer of decomposing leaves, but at 2 feet is very light grey sand as in the other communities.

Myoporum insulare Association.—This community consists of dense scrub about 6 feet in height and is confined to the southern end of the island where it covers an area of a few acres. Associated with this community are *Acacia cyclopis*, *Rhagodia baccata* and *Solanum simile*. Undergrowth species are *Eremophila brownii* and more rarely *Solanum nigrum*.

The soil is a very shallow dark grey sand overlying limestone.

Acacia heteroclita Association.—*Acacia heteroclita* is the main component of a stand of low scrub restricted to the limestone cliffs near Point Atwiek and northward. It stretches inland about a quarter of mile where it merges very gradually into the climax island vegetation.

The main associated plants are *Acacia rostellifera*, *Spyridium globulosum*, *Diplolaena dampieri*, *Leucopogon* spp., *Melaleuca pubescens* and *Exocarpus aphylla*. Below this storey there is a dense growth consisting mainly of *Lepidosperma squamatum* and less commonly of *Stipa variabilis*, *Phyllanthus calycinus* and *Acanthocarpus preissii*. *Westringia ridgii*, *Dodonaea aptera*, *Alyxia buxifolia*, *Acrotriche ovalifolia* and *Melaleuca pubescens* also occur near the cliff edge, these bushes often being prostrated and elongated by wind action.

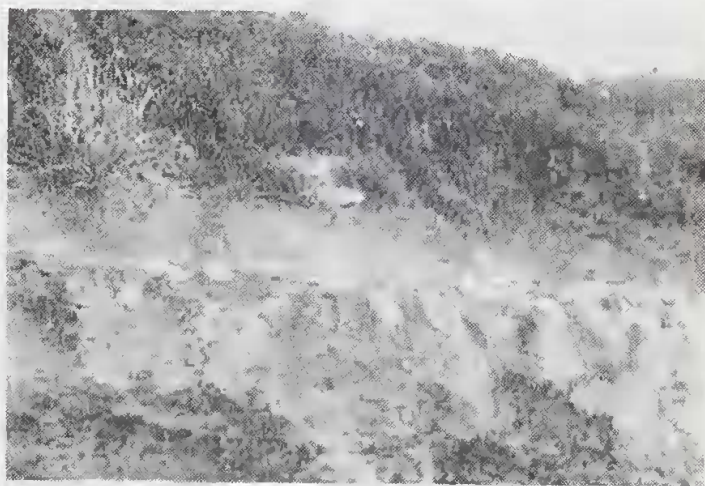


Fig. 10.—*Acacia heteroclita* association developed on shallow soil. Garden Island.

The soil is seldom more than a foot in depth and is fairly rich in organic matter (Fig. 10). This soil is similar to that on the south end of the island and chemical properties would be comparable.

Pittosporum phillyraeoides Association.—Near the south-west corner of Garden Island several small areas of *Pittosporum* scrub occur. They consist of thin straggly bushes about 4 feet 6 inches high with the foliage completely restricted to a small tuft on top. The canopy, though only 4-5 feet above the ground is very dense and completely closed. There is very little undergrowth and the soil, below a thick mat of leaves, consists of light brown gritty calcareous sand which becomes gradually lighter in colour with depth.

Seasonal Communities.—These communities are of considerable importance since they are the feeding grounds of the Garden Island Wallaby (*Protemnodon eugenii*). On the northern tip of the island the scrub gives way to an open area covered by *Asphodelus fistulosus*, *Anthericum divaricatum* and *Stipa variabilis*. The two former components die down to ground level in the summer months and then regenerate

in the spring. There seems to be a definite association between these plants and the introduced white land snails (*Bothriembrium bulla*), which congregate thickly on the stems without damaging the plant.

The second seasonal community, a mixed annual meadow occurs on the south end of the island and is developed on shallow dark grey sand overlying limestone. Some chemical properties of this soil are shown in Table I. The annual vegetation is rarely more than 2 inches high and is composed of *Euphorbia drummondii*, *Geranium pilosum*, *Erodium cicutarium* and *Poa* spp. In the late winter it forms a thick mat on the area between the *Acacia* scrub and the cliffs on the southern end of the island. The best development is in the valleys protected from the wind and salt spray. Other common plants here are *Anagallis arvensis*, *Tripteris clandestina*, *Solanum simile* and *S. nigrum*.

On the tops of the rocky headlands the vegetation is subject to salt water spray and possibly for this reason the annuals are almost absent. The more salt resistant plants *Carpobrotus acquilaterus*, *Stipa variabilis* and *Scirpus nodosus* make up most of the ground cover and even on these the effects of the salt are shown by necrotic spots. The shallow soil contains many foecal pellets which have been identified as those of insects, probably the larvae of a scarab beetle (Mr. J. Callaby, personal communications).

Littoral Vegetation.—This community is developed on the beaches, cliffs and partially fixed dunes bordering the island. The environmental conditions here are extreme—conditions which are generally recognised as being very unfavourable to plant growth. These include sand blast, desiccation, salt spray, intense light and highly calcareous sand as soil. It is understandable then that only specialised plants, characterised by waxy, hirsute and succulent leaves, can survive.

The limits of this zone are very poorly defined. It grades imperceptibly into the scrub. However, within the zone two fairly distinct habitats occur—the rocky cliffs and talus slopes and the sandy beaches.



Fig. 11.—Cliff side vegetation, Garden Island.

Generally the succulent plants are found on the rocky cliffs. Most common are *Carpobrotus acquilaterus* (Fig. 11), *Tetragonia implexicoma*, *T. zeheri*, *Wilsonia backhousii* and *Nitraria schoberi*. Where the cliff is not so steep other plants such as *Westringia rigida*, *Olearia axillaris*, *Alyxia buxifolia* and *Boronia alata* occur. Where the soil is deeper and a little more mature *Lepidosperma gladiatum* and *Scirpus nodosus* appear. In this habitat it seems that the wind is the main factor limiting species.

The sandy beaches have different environmental conditions. Salt spray is not so severe but light is very intense. Plants which can withstand sand blast such as *Calocephalus brownii*, *Angianthus cunninghamii*, *Arctotheca nivea* and *Spinifex hirsutus* are the most common. Here is opportunity for primary succession and on most beaches there is at least a rough zonation of vegetation.

Discussion of the Soil Properties

The soils of Garden Island are comparable to those of a considerable portion of the west coast of Western Australia and for this reason further discussion is warranted.

Smith (1951), referring to coastal soils in the Margaret River area and Speck (1952) working on similar soils in the vicinity of Perth, have emphasised the high content of calcium carbonate and the consequent alkaline reaction and high loss on ignition.

However, there has been little other recent work and so the present investigation, while not by any means complete, constitutes the first detailed examination of these soils. This work has the further advantage that the soils have been studied under conditions in which the soil-vegetation balance is practically undisturbed.

Table I shows the results of analyses for the major elements, the methods employed being those described by Piper (1947). Figures for phosphorus have been omitted because of lack of agreement between determinations using different analytical methods. Indications were that the surface horizons contained from 0.10 to 0.15% total phosphorus. This high figure may be due in part to calcium phosphate which occurs in some shells and foraminiferal tests.

The most important single factor affecting the soils is the extremely high content of calcium carbonate which commonly makes up 85% of the solum. This means that the reaction is always strongly alkaline and, in fact, the pH is below 8.0 only in the upper organic horizons. The high carbonate content serves to explain the discrepancy between the figures for sodium chloride and total soluble salts, the former usually being about 60-70% of the latter. In this case it is assumed that the total soluble salts include a considerable proportion of bicarbonate ions.

Chemical analyses show an unusually high fertility under virgin conditions in Western Australia. More important, it can be seen that the several communities have significantly

different levels, the soil supporting the *Acacia rostellifera* association having an extremely high level. The high nitrogen content in this soil suggests that *Acacia rostellifera* has nitrogen fixing properties.

A remarkable feature of these soils is the A₀₀ and A₀ horizons which commonly have a depth of 4 inches. The development and maintenance of these horizons is probably largely due to protection from fires since they are lacking on Rottneest Island where fires have been common. It is suggested also that the protection from sun and wind afforded by the dense canopy may keep surface conditions unfavourable for decomposition. Table I suggests that oxidation of the A₀ horizon has not proceeded very far. It is evident that the bulk of the nutrients are in and immediately below this horizon.

Oosting (1954) and Pidgeon (1950) have shown that the salinity of coastal soils is not as high as would be expected and suggest that soluble salts are removed rapidly, especially during the wet season. Pidgeon further suggests that it is the content of organic matter in the soil which determines the amount of soluble salts which can be retained. In the Garden Island soils, which were sampled after the main winter rains, the relation between these two components is very marked. Analysis of the results shown in Table I give a coefficient of 0.9425 ($p < 0.001$) for organic carbon with soluble salts and 0.9417 ($p < 0.001$) for nitrogen with soluble salts. Thus, taking the organic carbon and nitrogen content as a measure of the soil organic matter, there is a highly significant correlation. This fact needs to be considered in relation to the perennial beach plants, which are probably not halophytic even though they can survive saline conditions for short periods. The annual plants such as *Cakile maritima* and *Arctotheca nivea* are only present on the beaches during the winter when soluble salts would be quickly leached out.

It is of interest to speculate on the rate of soil formation on the calcareous dunes in Western Australia. Burges and Drover (1953) studied the rate of podzol development in beach dunes in New South Wales and concluded that a humus podzol had formed from dunes containing about 3.0% calcium carbonate in about 3,000 years. In the dunes under consideration here the content of calcium carbonate is in the vicinity of 80% and the time required for the soil to reach equilibrium would be much greater. Recent developments in radio-carbon dating of carbonates may enable the relative ages of the coastal dunes and limestone deposits to be established. In a highly calcareous soil a considerable proportion of the calcium carbonate could be leached away without a significant change in the apparent calcium carbonate content. It is evident that the proportion of calcium carbonate remaining to the apparent total weight of soil would remain fairly constant. For example a soil containing 90% calcium carbonate could lose 50% of its original weight and still show an apparent calcium carbonate content of 80%. This argument can be continued until the interstitial spaces become filled with the insoluble silica grains.

It seems probable that under the prevailing climatic conditions calcium carbonate would not remain in the solum, but would be leached out and redeposited in the vicinity of the ground water table leaving the upper part of the soil neutral or slightly acid in reaction. Such is the case in the Tuart (*Eucalyptus gomphocephala*) zone of the mainland where there is often ten feet of yellow sand overlying limestone (Speck, 1952). In many places along the mainland coast limestone occurs very near to the surface and it is assumed that this represents a truncated profile, the upper horizons of sand having been removed by wind. This will explain the crust of travertine which occurs so commonly.

Rottneest Island

An account of the overall geology and physiography of the islands has already been given, but further detail is necessary for Rottneest. For the most part it is composed of solid limestone in contrast with the unconsolidated dunes of Garden Island. Another feature is the low topographical level. The highest point is about 130' above sea level and, more important from the point of view of vegetation there are swamps and permanent lakes which provide completely different environmental conditions.

The relative proportions of species on the island has changed considerably since white man first landed on the island. This has been brought about by burning and clearing and to a lesser extent by the introduction of exotic species. However, the natural vegetation is more affected by the accidentally introduced species than by those intentionally introduced. *Asphodelus fistulosus* and *Anthericum divaricatum* which came originally from the Mediterranean, and *Euphorbia peplis* have spread all over the island. There are also several introduced grasses, e.g., *Poa australis* and *Polypogon maritimus*.

The present vegetation can be divided into several well defined communities and these will be discussed as follows:—

- (i) *Melaleuca pubescens* association (forest)
- (ii) *Acacia rostellifera* association (scrub)
- (iii) *Templetonia retusa* association (scrub)
- (iv) *Acacia cuneata* association (low scrub)
- (v) *Stipa-Acanthocarpus* community
- (vi) Halophytic communities
- (vii) Littoral vegetation

Description of the Communities

Melaleuca pubescens Association.—This tree forms pure stands of considerable area on Rottneest Island in contrast to Garden Island where only small clumps occur. It seems in some places that *Melaleuca pubescens* is the climax vegetation following a succession from swamps and lakes (Fig. 12) since on the higher ground surrounding these there is often a zone of *Melaleuca pubescens*. However, this tree also grows quite commonly on soils developed over limestone.

This community has a distinctive appearance with its clean straight boles and dense rounded crowns. In typically developed areas the trees are 30—35 feet high and have a dense interlocking canopy. Undergrowth is restricted to a sparse growth of *Stipa variabilis*.



Fig. 12.—*Melaleuca pubescens* association bordering Herschell Lake, Rottneest Island.

Acacia rostellifera Association.—This scrub varies in height from 8 to 15 feet and has a completely closed canopy. It is not now very widespread on the island, but appears to be a remnant of some former much larger community. It often occurs in the valleys but on higher ground around the lakes it appears to be a stage in the development of a climax.

There is evidence that *Stipa-Acanthocarpus* community is spreading at the expense of this association. Where the *Acacia* scrub has been burned or cleared the grass takes over before the *Acacia* can regenerate.

Templetonia retusa Association.—On Rottneest Island this association covers quite extensive areas mainly in the eastern sector and as on the mainland it is restricted to areas where limestone is at or near the surface (Fig. 13). The scrub is typically 6—8 feet in height and is fairly dense. Undergrowth is quite considerable and consists mainly of *Stipa variabilis* and *Senecio lautus*.

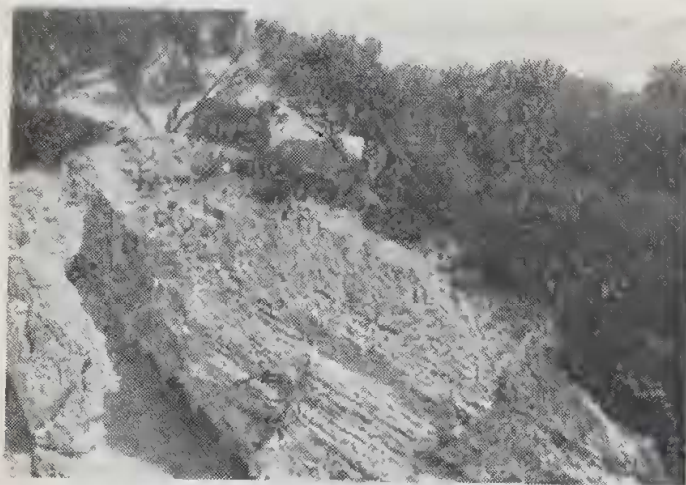


Fig. 13.—*Templetonia retusa* association growing on shallow soil over limestone, Rottneest Island.

Acacia cuneata Association.—This low scrub seldom exceeds four feet in height and is very dense. All the bushes are rounded and the branches reach right down to the soil surface allowing only restricted development of undergrowth.

The association is best developed on the western end of the island near the Neck where it grows on recently vegetated sand dunes. Although *Acacia cuneata* is the most abundant component, *Olearia axillaris* and *Westringia rigida* bushes together make up about 50% of the cover. *Scaevola* spp. also occur, especially near the shore. From the shore line there is a fairly well defined zonation of vegetation. *Spinifex longijolia* passes into *Olearia axillaris* which then merges into the *A. cuneata* scrub.

Stipa variabilis—*Acanthocarpus preissii* Community.—This is by far the most widespread community on the island and it is probable that the extent can be attributed to man's action in burning the *Acacia rostellifera* scrub (Fig. 14). The community grows apparently equally well on recently colonised sand dunes or on the sparse soil overlying limestone. Generally *Phyllanthus calycinus* is present on the younger soils and again, depending on edaphic factors, both



Fig. 14.—*Stipa variabilis*—*Acanthocarpus preissii* association which has developed where *Acacia* scrub has been cleared. Rottneest Island.

Thomasia cognata and *Guichenotia ledifolia* may occur. *Thomasia* grows on the shallow soils over limestone and *Guichenotia ledifolia* often occurs in the valleys. However, *Guichenotia* is not restricted to this community; in one place at least it appears to be a stage in the succession from swamp vegetation to *Melaleuca pubescens*. The community is the most important on the island from the viewpoint of food for animals and birds.

The Halophytic Communities.—It is the presence of this type of vegetation on Rottneest Island which makes it so different from Garden Island. The halophytic communities are developed on swamps and lakes which are mainly restricted to the eastern end of the island. The low lying regions give a distinctive appearance to the Rottneest landscape.

Zonation is clearly shown in these areas. Around each lake and swamp there are concentric bands of successively taller vegetation types (Fig. 15). In fact this may be true plant succession.



Fig. 15.—Zonation of vegetation bordering a swamp on Rottneet Island. Zones from the water's edge are *Salicornia blackiana*, *Atriplex paludosa*, *Scirpus nodosus*, *Solanum simile* and *Stipa variabilis*.

On the lowest levels the soil is saline (6.25% sodium chloride) calcareous mud containing algal remains and gastropod shells. *Wilsonia humilis* and *Salicornia blackiana* occur on this soil which is waterlogged for the greater part of the year. There is a sharp transition from this zone to a thick mat of *Salicornia* below which the soil, although damp, is not always waterlogged. This soil has 3.3% sodium chloride. The next zone varies considerably in different localities. In some cases the *Salicornia* merges into an *Arthrocnemum bidens* zone and thence into *Melaleuca pubescens* or *Acacia rostellifera* zone. This is generally the case in the swampy areas. However, around the lakes the zone following *Salicornia* is usually a narrow band of *Atriplex paludosa*. Rarely the *Atriplex* may be absent and the *Salicornia* ends abruptly giving way to a dense *Scirpus nodosus* or *Scirpus nodosus-Gahnia trifida* community. The soil in this zone is brown calcareous sand in which the salt content is negligible.

In one instance the *Arthrocnemum bidens* passes into a poorly defined zone of *Stipa variabilis* in which *Guichenotia ledifolia* is also present. However, this may be lacking and either *Melaleuca pubescens* or *Acacia rostellifera* may grow right down to the edge of the swamp. Around the lakes the sequence is more constant and the *Scirpus-Gahnia* zone passes gradually into a narrow band of *Solanum simile*. Where the ground begins to rise this last band disappears and, depending on whether or not the area has been burned, *Stipa-Acanthocarpus* or *Melaleuca pubescens* occur.

Littoral Vegetation.—These communities are similar in all respects to those already described on Garden Island.

Carnac Island is about two miles north of Garden Island. It forms roughly a square of about 38 acres in area. Except for a sheltered sandy beach on the east and two tiny beaches on the west side the island is bounded by steep limestone cliffs. The highest point is 60 feet and there is very little of the island below 25 feet in height. The uniform topography means that most of the island is exposed to the wind and this fact is reflected in the vegetation. There is no fresh water on the island.

It is to be expected that Carnac Island situated as it is between Garden Island and Rottneet Island would have similar vegetation. However, being such a small island on which no part is more than 200 yards from the sea, it is natural that the dominant plants would be those which are found only on the borders of the larger islands.

The recognisable communities, which are shown in Fig. 16 are as follows:—

- (i) *Acacia rostellifera*—*Olearia axillaris* association (scrub)
- (ii) *Olearia axillaris*—*Scaevola crassifolia* association (low scrub)
- (iii) *Frankenia pauciflora*—*Rhagodia baccata* association (low scrub)
- (iv) *Rhagodia baccata* association (low scrub)
- (v) *Nitraria schoberi* association (low scrub)
- (vi) *Scaevola crassifolia* — *Calocephalus brownii* association (low scrub)
- (vii) *Carpobrotus aequilaterus*—*Tetragonia* spp.—*Suaeda maritima* mat

(a) Description of the Communities

Acacia rostellifera—*Olearia axillaris* Association.—This community abuts on to the eastern beach and extends about halfway across the island. It appears to be the climax vegetation for this island. *Acacia rostellifera* is the main component, but *Olearia axillaris* is spread uniformly throughout. *Clematis microphylla* does occur here but is never well developed. Undergrowth consists of *Bromus gussonii* and *Lepidosperma gladiatum*.

The soil consists of calcareous fine sand very low in organic matter.

This community merges imperceptibly into the shoreward zone of *Olearia*—*Scaevola* scrub.

Olearia axillaris—*Scaevola crassifolia* Association.—This is the most variable community on the island, but the two main components occur fairly uniformly throughout (Fig. 17). *Rhagodia baccata* becomes more common near the shoreward cliffs.

The soil is light grey calcareous sand with limestone 8—12 inches below the surface.

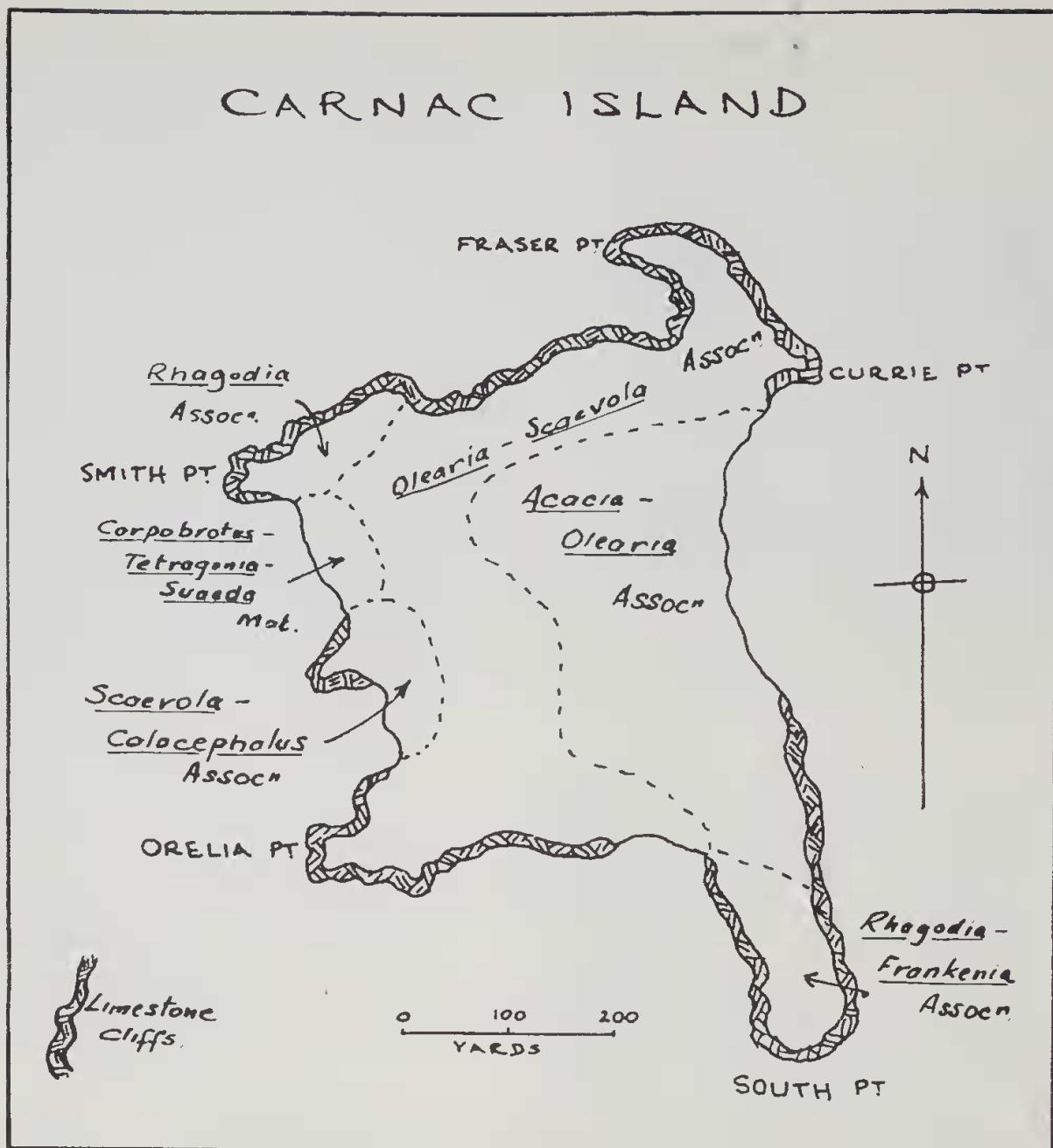


Fig. 16.—The plant communities on Carnac Island.

Frankenia pauciflora—*Rhagodia baccata* Association.—This is a very distinct and sharply defined community restricted to South Point. It is typically 12—18 inches in height and completely covers the soil. The soil consists of a few inches of dark brown calcareous sand overlying travertinized limestone (Fig. 18).

Rhagodia baccata Association.—This occupies only a small area near Smith Point (Fig. 19) It grows right up to the cliff edge on the north-west and extends about 50 yards landwards.

It is about two feet in height and is quite dense. The soil is fairly deep and is coarse textured throughout.

Nitraria schoberi Association.—On Carnac Island *Nitraria schoberi* forms a dense tangled scrub all along the talus slopes of the cliffs on the northern side. *Rhagodia baccata* occurs but only rarely. The very loose sandy soil of the talus is stabilised mainly by the cover of *Nitraria*.



Fig. 17.—*Olearia axillaris*—*Scaevola crassifolia* scrub in the foreground merging into *Acacia rostellifera*—*Olearia axillaris* scrub in the background, Carnac Island.



Fig. 18.—*Frankenia pauciflora*—*Rhagodia baccata* association, Carnac Island.



Fig. 19.—*Rhagodia baccata* scrub on a talus slope, Carnac Island.

Scaevola crassifolia—*Calocephalus brownii* Association.—On the western shore between the two beaches is a small area where *Calocephalus brownii* extends back from the coast and merges with the *Olearia*—*Scaevola* scrub to form a separate community. This may be only a variant of the *Olearia*—*Scaevola* scrub, but it appears different enough to warrant separate consideration. *Salicornia blackiana* forms a mat over a small area on the point between the beaches.

Carpobrotus aequilaterus—*Tetragonia* spp.—*Suaeda maritima* Mat.—Fringing the larger of the two western beaches is a thick mat of succulent vegetation. This extends back about 50 yards from the beach. Besides the three main components *Enchylaena tomentosa* occurs frequently. The bank is quite steep but the loose sand is held firmly by the vegetation.

The Mainland

The mainland adjacent to the islands, with an expanding city in its immediate hinterland, has suffered many changes in respect to its vegetation. However, there are remnants of the original vegetation at various points between Point Peron and North Beach and it is the vegetation of these areas which will be compared with that of the islands.

Point Peron, which was formerly a rocky island is now joined to the mainland by blown sand (Fairbridge, 1948). It is controlled by the same environmental conditions as the islands and this is reflected in the vegetation. However, there are some important differences. As would be expected there has been an influx of introduced species such as *Euphorbia* spp., *Bromus gussonii*, *Solanum sodomaeum*, *Aster subulatus*, *Sporobolus virginicus* and *Tripteris clandestina*.

The natural vegetation, though structurally the same as that of the islands, differs in that certain species common to the islands are absent. The most important of these are *Melaleuca pubescens*, *Guichenotia ledifolia* and *Lasiopetalum angustifolium*. Species common to the understoreys of the *E. gomphocephala* and *E. marginata* associations do not occur on Point Peron. It is assumed then that the absence of these plants on the islands is not due to isolation, but environmental conditions.

The coastal strip between Fremantle and Reckingham was probably originally covered by dense *Acacia rostellifera* scrub similar to that on Garden Island. At present it is much denuded by clearing and fires, but it appears to differ only in that *Xanthorrhoea preissii* occurs commonly throughout. The remnants of *Callitris robusta* scrub near Naval Base also shows the similarity of this strip to the island vegetation. Relics of a similar vegetation are to be seen along cliff sides of the Swan River at Freshwater Bay, Mosman Bay and Blackwall Reach.

Further to the north at Cottesloe, City Beach, Scarborough and North Beach the vegetation is different, the mature tuart and jarrah forest approaching much nearer to the shoreline, although there is an area of dense *Acacia rostellifera* scrub between City Beach and Scarborough.

One of the most striking features of the beaches of the mainland, particularly City Beach and Scarborough, is the presence of *Arctotheca nivea*, which is most active in stabilising the sand (Fig. 20). This plant keeps pace with the banking sand and in most places the bank is several feet in height. It may well be that this is the first stage in plant succession since this zone is followed by successive zones of *Spinifex hirsutus* and *Olearia axillaris*—*Scaevola* spp. before reaching the low scrub which is probably the climax dune vegetation. The scrub is made up principally of *Scaevola* spp., *Rhagodia baccata*, *Myoporum insulare*, *Olearia axillaris*, *Scirpus nodosus*, *Lepidosperma gladiatum* and the creepers *Cassytha glabella* and *Hardenbergia comptoniana*.



Fig. 20.—Beach sand stabilised by *Arctotheca nivea*, City Beach.

Alyxia burifolia and *Dodonaea aptera* do not occur in the beach vegetation of the mainland. These are very common on the islands, but apparently occur on the mainland only on Point Peron. Within a short distance of the shoreline in the City Beach-Scarborough area occur many plants not usually associated with beach vegetation. These are *Santalum acuminatum*, *Hibbertia* spp., *Melaleuca acerosa*, *Oxylobium capitatum*, *Gompholobium tomentosum*, *Acacia pulchella* and *Tersonia brevipes*. The presence of these is a reflection of more mature soil conditions.

It is not until the *E. gomphocephala* zone is reached that significant numbers of Proteaceous and Leguminous plants are found. *Grevillea crithmifolia* and *Petrophila serruriae* occur on the seaward fringe of this zone and then *Banksia* spp. and *Stirlingia latifolia* are associated with the tuart. *Casuarina fraseriana* also occurs as part of the understorey of the tuart, but is not found nearer the shoreline. *Agonis flexuosa* commonly grows on the calcareous dunes of the mainland but is not found on the islands.

It is of interest to note that the coastal vegetation contains many genera and even species which occur much further inland in the Ereman Province. It is evident that the habitats have

no obvious common environmental factor, although Gardner (1942) points out that the soils which support these plants are either physically or physiologically dry. It is likely that the solution to this problem will be found only in a study of the physiology of the plants concerned. The presence of calcium carbonate in the profile may be part of the answer, but other factors will also contribute.

Discussion

The vegetation of the islands has distinctive features both structurally and floristically. The undisturbed vegetation as already described consists of dense almost impenetrable scrub in which the upper storey is completely closed and the understorey very sparse or absent. This is in striking contrast to the jarrah (*E. marginata*) and tuart (*E. gomphocephala*) associations of the mainland which have an open tree layer and a rich and varied understorey of small shrubs and harsh woody monocotyledons. These associations are however developed on mature soils such as do not exist on the islands.

The distribution of species both on the islands and the mainland can, with some exceptions, be explained by habitat rather than insularity. Thus the protected sandy beaches on the eastern side of Garden Island, Thompson's Bay on Rottneest Island and Mangles Bay near Rockingham are characterised by a zone of *Spinifex longifolia* which grows at the foot of a low fore-dune, the scrub approaching very near to the beach. The exposed beaches on the western sides of the islands, Shoalwater Bay near Rockingham and metropolitan beaches on the mainland, have a much steeper bank, which is stabilised by *Scirpus nodosus*, *Lepidosperma glabratum* and then by *Olearia axillaris* and *Scaevola* spp. On the seaward side of the bank *Spinifex hirsutus* and *Arctotheca nivea* are the only plants which can withstand the sand blast, although there may occasionally be *Salsoia kali* and *Cakile maritima*.

The rocky cliffs and headlands on the western sides of the islands, and along the mainland coast between the metropolitan beaches, also have a characteristic vegetation—both in species and habit. The salt spray tolerant plants, *Carpobrotus*, *Tetragonia*, *Suaeda*, *Enchylaena* and *Frankenia pauciflora* are very commonly seen clinging to the rocks and *Nitraria* and *Rhagodia* where there is a little more soil. *Calocephalus*, *Angianthus* and *Scaevola crassifolia* are common along the tops of exposed cliffs, but apparently require a few inches of soil to survive. There are some larger bushes such as *Alyxia buxifolia*, *Dodonaea aptera* and *Westringia rigida*, which, when present in this habitat, are wind-shorn and prostrate. Thus on Carnac Island, which is principally bordered by rocky cliffs and of relatively small extent, it is found that the most common plants are *Nitraria*, *Rhagodia*, *Olearia axillaris* and the succulent plants.

The stable dunes on the islands and on parts of the mainland support a dense growth of tall scrub or scrub. This grades shoreward into the low scrub of the recently colonised dunes or the scattered prostrate plants of the tops of the exposed limestone cliffs.

On Rottneest Island and on parts of the mainland coast the limestone comes very near to the surface and such areas are characterised by *Templetonia retusa* and *Thomasia cognata*. *Templetonia retusa* does not occur on Garden Island although there are many places where it would be expected.

Having established that the species distribution within any one area is dependent on habitat, it remains to explain the overall distribution of species, and for the explanation it is necessary to use palaeo-geographical evidence. It has been suggested (Fairbridge 1948) that the whole of the continental shelf became dry land during the period corresponding to the Würm exposure of Europe. This would allow large areas of aeolianite to accumulate and so for a short time coastal conditions extended far beyond the present shoreline allowing migration of typical coastal species. In the ensuing period towards the close of the Pleistocene, the level of the sea rose gradually, the higher parts of the aeolianite being cut off from the mainland. This explains why some of the same species are found on all the islands and the mainland, although there are anomalies such as the absence of *Melaleuca pubescens* on the coast adjacent to the islands.

The absence from the islands of such characteristic Australian families as the Proteaceae and Xanthorrhoeaceae and many of the Myrtaceae is at first sight very striking. However, it is evident that these families are not found on the mainland where conditions approximate to those on the islands. The vegetation development under similar conditions in these two areas is substantially the same and it is the environment rather than isolation which has restricted migration.

Acknowledgments

The work described in this paper has been carried out as part of the ecological research programme of the Botany Department of the University of Western Australia under the supervision of Miss A. M. Baird. The author wishes to acknowledge his indebtedness to Dr. B. J. Grieve, Head of the Department, who has given encouragement and advice throughout the work and who has critically revised the manuscript. Thanks are due also to other members of Botany Department staff for generous assistance; to Mr. C. A. Gardner (Government Botanist) and Mr. R. D. Royce of the State National Herbarium, Perth, who checked many of the plant names; to Dr. J. Gentili (Economics Department, University) who supplied figures relating to rainfall effectiveness and evapo-transpiration; to Dr. K. Sheard (C.S.I.R.O. Division of Fisheries) who assisted with transport to the islands; to Dr. D. P. Drover of the Institute of Agriculture, University of Western Australia, for advice and assistance on soil analysis; to the staff of the Survey Section at Karrakatta Army Barracks, who supplied aerial photographs and large scale maps of Garden Island; and finally to the lessee of Garden Island, Mr. F. Oliver, for valuable help and advice.

References

Appendix 1—continued.

Beadle, N. C. W. and Costin, A. B. (1952).—Ecological Classification and Nomenclature. *Proc. Linn. Soc. N.S.W.* 77: 61-82.

Burges, A. and Drover, D. P (1953).—The Rate of Podzol Development in Sands of the Woy Woy District, N.S.W. *Aust. J. Bot.* 1: 83-94.

Fairbridge, R. W. (1948).—Notes on the Geomorphology of the Pelsart Group of Houtman's Abrolhos Islands. *J. Roy. Soc. W. Aust.* 33: 1-43.

Fairbridge, R. W. (1950).—The Geology and Geomorphology of Pt. Peron, Western Australia. *J. Roy. Soc. W. Aust.* 34: 35-72.

Gardner, C. A. (1942).—The Vegetation of Western Australia with special references to the Climate and Soils. *J. Roy. Soc. W. Aust.* 28: 11-87.

Gentilli, J. (1948).—Two Climatic systems applied to Australia. *Aust. J. Sci.* 11: 13-16.

Harvey, W. H. (1854).—Some Account of the Marine Botany of the Colony of Western Australia. *Roy. Irish Acad. Trans.* 22: 522-566.

Heeres, J. E. (1899).—"The Part Borne by the Dutch in the Discovery of Australia 1606-1765." (Luzac and Company: London.)

McKnight, T. (1949).—Efficiency of Isolates of Rhizobium in the Cowpea Group. *Qd. J. Agric. Sci.* 6: 61-76.

Oosting, H. J. (1954).—Ecological Processes and Vegetation of the Maritime Strand in the Southeastern United States. *Bot. Rev.* 20: 226-276.

Pidgeon, Irma M. (1940).—The Ecology of the Central Coastal Area of New South Wales. III. *Proc. Linn. Soc. N.S.W.* 65: 221-249.

Piper, C.S. (1947).—"Soil and Plant Analysis." (University of Adelaide: Adelaide.)

Smith, R. (1951).—Soils of the Margaret and Lower Blackwood Rivers, W.A. Coun. Sci. Industr. Res. Aust. Bulletin 262.

Speck, N. H. (1952).—"Plant Ecology of the Metropolitan Sector of the Swan Coastal Plain." (Thesis: University of Western Australia.)

Teichert, C. (1947).—Late Quarternary Changes in the Sea Level at Rottnest Island, Western Australia. *Proc. Roy. Soc. Vict.* 59: 63-79.

Thorntwaite, C. W. (1931).—The Climates of North America. *Geogr. Rev.* 21: 631-655.

Thorntwaite, C. W. (1948).—A Rational Classification of Climate. *Geogr. Rev.* 38: 55-94.

Wilson, J. K. (1939).—A Relation between Pollination and Nodulation of the Leguminosae. *J. Amer. Soc. Agron.* 31: 159-170.

Zeuner, F. E. (1945).—"The Pleistocene Period, its Climate, Chronology and Faunal Succession." (Ray Society: London.)

Zeuner, F. E. (1946).—"Dating the Past: An Introduction to Geochronology." (Methuen: London.)

Appendix I

Distribution of Plant Species on the Coastal Islands

	Rottnest Island	Garden Island	Carnac Island
Cupressaceae			
<i>Callitris robusta</i> (R.Br.) Mirb.	x	x	
Typhaceae			
<i>Typha angustifolia</i> Linn.		x	

	Rottnest Island	Garden Island	Carnac Island
Gramineae			
<i>Spinifex hirsutus</i> Labill.	x	x	
<i>Spinifex longifolius</i> R.Br.	x	x	x
<i>Stipa variabilis</i> Hughes ...	x	x	
<i>Polypogon maritimus</i> Willd.	x		
<i>Polypogon monspeliensis</i> (L.) Desf.	x		
* <i>Avena fatua</i> Linn.	x	x	x
<i>Poa annua</i> Linn. ..	x	x	
* <i>Poa caespitosa</i> Forst.	x	x	
* <i>Bromus gussonii</i> Parl.	x	x	x
Cyperaceae			
<i>Scirpus antarcticus</i> Linn.		x	
<i>Scirpus nodosus</i> Rottb.	x	x	x
<i>Lepidosperma gladiatum</i> Labill.	x	x	x
<i>Lepidosperma squamatum</i> Labill.	x	x	
<i>Gahnia trifida</i> Labill.	x		
Liliaceae			
<i>Thysanotus patersoni</i> R.Br.	x	x	
* <i>Asphodelus fistulosus</i> Linn.	x	x	
<i>Asparagus asparagoides</i> Wight		x	
* <i>Anthericum divaricatum</i> Jacq.	x	x	
<i>Dianella revoluta</i> R.Br.	x	x	
<i>Acanthocarpus preissii</i> Lehm.	x	x	
Amaryllidaceae			
<i>Conostylis candicans</i> Endl.	x	x	
Orchidaceae			
<i>Eriochilus tenuis</i> Lindl.		x	
Urticaceae			
<i>Parietaria debilis</i> Forst.		x	
Santalaceae			
<i>Exorcarpus aphylla</i> R.Br.	x	x	
<i>Leptomeria preissiana</i> (Miq.) D.C.	x	x	
Leranthaceae			
<i>Loranthus miraculococus</i> (Miq.) var. <i>melaleuca</i> (Tate) Blakely			x
Polygonaceae			
* <i>Emex australis</i> Steinh.	x	x	
Chenopodiaceae			
<i>Rhagodia baccata</i> (Labill.) Miq.	x	x	x
<i>Atriplex isitidia</i> Miq.	x	x	x
<i>Atriplex paludosa</i> R.Br.	x		
<i>Salsola kali</i> Linn. ..	x	x	x
<i>Salicornia blackiana</i> Ulbrich.	x	x	x
<i>Arthrocnemum bidens</i> Nees.	x		
<i>Enchylacna tomentosa</i> R.Br.	x	x	x
<i>Suaeda maritima</i> (R.Br.) Miq.	x	x	x
* <i>Chenopodium murale</i> Linn.	x	x	
Aizoaceae			
* <i>Tetrogonia zeheri</i> Fenzl. ex Harv. et Sond.	x	x	x
<i>Tetrogonia implexicoma</i> (Miq.) Hook.	x	x	x
<i>Carpobrotus aequilaterus</i> N.E.Br.	x	x	x
<i>Cryophytum crystallinum</i> (L.) N.E.Br.	x		
Raunculaceae			
<i>Clematis microphylla</i> D.C.	x	x	x
Lauraceae			
<i>Cassytha glabella</i> R.Br.	x	x	
Cruciferae			
<i>Cakile maritima</i> Scop.	x	x	x
Pittosporaceae			
<i>Pittosporum phillyraeoides</i> D.C.	x	x	
Mimosaceae			
<i>Acacia rostellifera</i> Benth.	x	x	x
<i>Acacia heteroclita</i> Meissn.	x	x	
<i>Acacia cyclops</i> A. Cunn.		x	x
<i>Acacia cyanophylla</i> Lindl.	x	x	
<i>Acacia cuneata</i> A. Cunn.	x		

	Rottnest Island	Garden Island	Carnac Island
Papilionaceae			
<i>Hardenbergia comptoniana</i> R.Br.	x	x	
<i>Templetonia retusa</i> R.Br.	x	
Geraniaceae			
<i>Geranium pilosum</i> Forst.	x	
<i>Pelargonium australe</i> Wild.	x	x
* <i>Erodium cicutarium</i> (L.) L'Her.	x	x	
Zygophyllaceae			
<i>Nitraria schoberi</i> Linn.	x	x
Rutaceae			
<i>Boronia alata</i> Smith	x	x
<i>Diplolaena dampieri</i> Desf.	x	x
Polygalaceae			
<i>Comesperma integerrimum</i> Endl.		x	
<i>Comesperma confertum</i> Labill.		x	
Euphorbiaceae			
<i>Phyllanthus calycinus</i> Labill.	x	x	
* <i>Euphorbia drummondii</i> Boiss	x	
* <i>Ricinus communis</i> Linn.		
<i>Beyeria viscosa</i> (Labill.) Miq.	x	
Stackhousiaceae			
<i>Stackhousia pubescens</i> A. Rich.	x		
Sapindaceae			
<i>Dodonaea aptera</i> Miq.	x	
Rhamnaceae			
<i>Spyridium globulosum</i> (Labill.) Benth.	x	x
Sterculiaceae			
<i>Lasiopetalum angustifolium</i> W. V. Fitz.	x	
<i>Guichenotia ledifolia</i> J. Gray	x	
<i>Thomasia cognata</i> Steud.	x	
Frankeniaceae			
<i>Frankenia pauciflora</i> D.C.	x	x
Myrtaceae			
<i>Melaleuca pubescens</i> Schau.	x	x
<i>Melaleuca huegelii</i> Endl.	x	x
Onagraceae			
<i>Epilobium glabellum</i> Forst.	x	
Umbelliferae			
<i>Didiscus pilosus</i> Benth.	x	
<i>Didiscus coeruleus</i> D.C.	x	
Epacridaceae			
<i>Leucopogon richei</i> (Labill.) R.Br.	x	x	
<i>Leucopogon racemosus</i> R.Br.	x	x	
<i>Acrotriche ovalifolia</i> R.Br.	x	x

	Rottnest Island	Garden Island	Carnac Island
Gentianaceae			
<i>Erythraea centaurium</i> Pers.	x	x
Frimulaceae			
* <i>Anagallis arvensis</i> Linn.	x	x
<i>Samolus repens</i> (Forst.) Pers.	x	
Apocynaceae			
<i>Alyxia buxifolia</i> R.Br.	x	x
Convolvulaceae			
<i>Wilsonia humilis</i> R.Br.	x	
<i>Wilsonia backhousii</i> Hook.	x	
Labiatae			
<i>Westringia rigida</i> R.Br.	x	x
Solanaceae			
<i>Solanum nigrum</i> Linn.	x	x
<i>Solanum simile</i> F. Muell.	x	
Scrophulariaceae			
<i>Dischisma capitatum</i> (Thunb.) Chois.	x	x
Orobanchaceae			
<i>Orobanche australiana</i> F. Muell.	x	x	x
Myoporaceae			
<i>Myoporum insulare</i> R.Br.	x	x
<i>Myoporum viscosum</i> R.Br.	x	
<i>Eremophila brownii</i> F. Muell.	x	x
Lobeliaceae			
<i>Lobelia tenuior</i> R.Br.	x	x
Goodeniaceae			
<i>Scaevola crassifolia</i> Labill.	x	x
Compositae			
<i>Olearia axillaris</i> (D.C.) F. Muell.	x	x	x
<i>Senecio lautus</i> Soland.	x	x
<i>Calocephalus brownii</i> (Cass) F. Muell.	x	x
* <i>Arctotheca nixa</i> (Less) Leeuwin	x	x	
* <i>Cryptostemma calendulaeum</i> (Linn.) R.Br.	x	
<i>Athrixia pulverulenta</i> (Lindl.) Druce	x	
<i>Hypochoeris glabra</i> Linn.	x	
* <i>Sonchus asper</i> Hill	x	x
* <i>Sonchus oleraceus</i> Linn.	x	x
* <i>Tripteris clandestina</i> Less.	x	x
* <i>Erigeron crispens</i> Ponnet	x	
* <i>Angianthus humifusus</i> (Labill.) Benth.	x	
<i>Angianthus cunninghamii</i> (D.C.) Benth.	x	x
* <i>Inula graveolens</i> Desf.	x	

* Introduced species.

Appendix II

Climatological Data, Rottnest Island, W.A.

	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Year.
Absolute Max. Temp. °F.	101.0	99.0	93.0	87.0	78.5	72.4	69.6	71.4	80.0	88.0	92.2	97.4	101.0
Mean Max. Temp. °F.	78.2	78.8	76.6	73.5	68.0	64.1	62.4	63.0	64.8	67.2	72.0	75.4	70.1
Mean Temp.	71.6	72.2	69.4	67.5	62.9	59.6	57.8	58.1	59.5	61.6	65.8	69.1	64.6
Mean Min. Temp. °F.	64.9	65.5	64.1	61.6	57.9	55.1	53.2	53.1	54.2	55.8	59.5	62.8	59.0
Absolute Min. Temp. F.	56.0	55.0	53.8	51.5	48.2	45.8	45.0	44.0	46.0	48.0	50.0	54.0	44.0
Mean Daily Range	13.3	13.3	12.5	11.9	10.1	9.0	9.2	9.2	10.6	11.4	12.5	12.6	11.4
Rel. Hum., 9 a.m. (%)	63	63	67	69	73	76	76	74	73	70	66	63	70
Rel. Hum., 3 p.m. (%)	64	64	65	64	67	69	70	68	69	67	66	65	67
Cloud, 9 a.m. (tenths) ...	3.7	4.0	4.4	5.1	6.0	6.4	6.2	6.0	5.7	5.5	4.8	4.1	5.2
Cloud, 3 p.m. (tenths) ...	3.3	3.7	4.0	4.9	5.9	6.3	6.2	5.8	5.5	5.1	4.2	3.5	4.8
Mean Sat. Deficit (ins. Hg)	0.289	0.285	0.229	0.202	0.152	0.124	0.117	0.126	0.142	0.176	0.223	0.271	0.195
Rainfall (ins.)	0.23	0.38	0.56	1.44	4.40	6.49	5.99	4.42	2.56	1.51	0.56	0.38	28.89
Wet Days (No.)	2.2	1.8	5.6	9.1	13.6	19.3	22.0	16.8	15.0	11.1	6.9	5.6	129
Effectiveness (Est.)	0.3	0.5	0.6	1.9	7.1	11.9	11.2	7.9	4.6	2.5	0.9	0.5	49.5
Evapo-transpiration (Est.)	4.66	4.02	3.91	2.98	2.25	1.68	1.52	1.66	1.94	2.57	3.40	4.13	34.72

TABLE I.

Chemical Properties of Garden Island Soils

Profile No.*	Depth (ins.)	pH.	Percentage CaCO ₃ .	Percentage NaCl.	Percentage Total Soluble Salts.	Percentage Total Organic Carbon.	Percentage Total Nitrogen.	C/N.
1	A ₀	7.4	23.5	0.012	0.09	26.8	1.46	18.4
	0-2	7.9	59.2	0.008	0.06	13.6	0.58	23.4
	2-9	8.2	75.5	0.008	0.04	2.9	0.19	15.2
	9-19	8.4	78.3	0.002	0.04	1.9	0.15	12.7
	19-32	8.4	82.9	0.006	0.04	1.9	0.08	23.8
2	A ₀	7.2	41.7	0.010	0.09	21.8	0.94	23.2
	0-9	8.3	76.8	0.006	0.04	3.5	0.18	19.5
	9-18	8.5	85.3	0.004	0.04	1.0	0.09	11.1
	18-30	8.6	88.7	0.006	0.03	0.6	0.03	20.0
3	0-4	8.3	85.5	0.002	0.04	3.6	0.19	25.3
	4-11	8.5	88.7	0.002	0.03	1.4	0.07	20.0
	11-29	8.6	90.0	0.002	0.02	1.2	n.d.	—
4	0-8	8.2	69.8	0.010	0.05	4.6	0.40	11.5

- * 1 Soil under *Acacia rostellifera* association.
 2 Soil under *Callitris robusta* association.
 3 Soil under *Melaleuca hurgelii* association.
 4 Shallow soil on limestone. Seasonal vegetation.